Climate change effects on spawning phenology in a coolwater fish, the yellow perch (*Perca flavescens*)

Honors Research Thesis

Presented in Partial Fulfillment of the Requirements for graduation "with Honors Research Distinction" in the undergraduate colleges of The Ohio State University

by
Breanna Humbarger

The Ohio State University
April 2013

Project Advisor: Professor Elizabeth A. Marschall, Department of Evolution, Ecology, and Organismal Biology

Introduction

Understanding how the timing (or phenology) of important life history events, such as reproduction, are controlled by ambient temperature is a major focus of climate change research. Studies in terrestrial environments indicate many migratory bird species arrive earlier at spring nesting grounds and many plant species bloom earlier in response to early spring warming (Walther et al. 2002). In aquatic environments, warmer water temperatures accelerate metabolic processes, which in turn accelerate growth and reproductive development, resulting in shifts in timing of certain behaviors, such as spawning. Evidence suggests the timing of reproduction has important consequences for early-life growth and survival in fish, which directly affect population dynamics (Cushing 1990).

While many long-term phenology studies exist for terrestrial species; equivalent long-term studies of fish reproductive events are rare (Genner et al. 2009). Yellow perch *Perca flavescens* (economically and ecologically important across North America) is a coolwater fish species that typically spawns during April - May in Lake Erie, during a time when temperatures are highly variable from year to year. Previous laboratory studies indicate ambient spring temperature may have a minimal effect on the onset of yellow perch spawning (Kayes and Calbert 1979); however, this hypothesis has not been tested in the field.

In a laboratory experiment conducted in 1976 by Kayes and Calbert (1979), increasing day length and water temperature had little effect on timing of spawning when applied in February but decreased the variability in timing of spawning when applied in the spring. They hypothesized that the initiation of yellow perch spawning was more dependent on intrinsic female maturational state than on photoperiod-temperature shifts, which could increase (if applied during the typical time of spawning) or decrease (if applied too early) the predictability of yellow perch spawning. Ultimately, Kayes and Calbert (1979) determined that neither photoperiod nor temperature manipulation could speed the onset of spawning. I sought to determine if the initiation of yellow perch spawning in the field was equally insensitive to photoperiod-temperature cues during the spring.

Specifically, I sought to understand the factors that control the phenology of yellow perch spawning in Lake Erie. My primary objective was to determine the relationship between spawning timing and spring water temperatures by quantifying the reproductive status of female yellow perch during weekly spring sampling events during the spawning season. Ultimately, I will discuss the match/mismatch hypothesis, which relates survival to the match between larval occurrence and that of the production of their food (Beaugrand et al. 2003). I will also relate findings to those from other fish species, highlighting similarities, differences, and implications for management in a changing climate.

Methods

Study System

Lake Erie is the southernmost lake in the Laurentian Great Lakes system and is comprised of three distinct basins (west, central, and eastern basins) that vary in depth and productivity. Generally, the basins increase in depth and decrease in productivity from west to east. The west basin is the shallowest of the three basins and the most productive. The Great Lakes region has been experiencing a warming trend during the past 60 years, during which the average winter duration (measured as the annual number of days below freezing recorded at Toledo, OH) has decreased by approximately 30 days (T. Farmer unpublished data). In response to this winter warming, annual maximum ice cover across the Great Lakes has decreased 71%

over the last 38 years (Wang et al. 2010). The arrival of ice free conditions in the spring is occurring progressively earlier across the Great Lakes region (Magnuson 2010), indicating that the frequency of short mild winters, followed by early spring warming, is increasing.

Field Collections

Female yellow perch were captured in western Lake Erie during weekly sampling trips in April and May 2010-2012 across two nearshore-to-offshore transects near Sandusky, Ohio. Bottom trawling was conducted aboard either the Ohio Division of Wildlife's RV Explorer or the U. S. Geological Survey's RV Musky II. Trawl sites were stratified by depth along nearshore-to-offshore transects, with two trawls conducted within depth intervals of 20-25, 26-30, 31-35, and ≥36 ft. At each site, yellow perch were sampled during a 10-min bottom trawl (see Tyson et al. 2006 for trawl dimensions and trawling speeds for each vessel). In total, 195 trawls were conducted over the course of the study, and all were conducted during daylight hours.

To relate environmental variables to spawning activity of yellow perch, abiotic water column profiles of temperature and dissolved oxygen were collected concurrently with bottom trawling using a YSI® 550A handheld meter. All yellow perch collected were euthanized in the field, placed on ice, and returned to the Aquatic Ecology Laboratory in accordance to guidelines established by the American Veterinary Medical Association (2007).

All yellow perch were weighed (nearest g) and measured for total length (nearest mm). Each female was dissected and classified as either i) immature [immature ovaries with no egg development], ii) gravid [mature with eggs, but not ready to spawn], iii) flowing [actively releasing eggs at time of capture], or iv) spent [post-spawn] based on visual observation following Treasurer and Holiday (1981). As it is not feasible to observe yellow perch spawning in Lake Erie, these classifications of reproductive status of captured fish were used to infer the progression of spawning throughout spring.

Statistical Analysis

From the trawl data, for each week of sampling, we estimated 1) catch per unit effort (CPUE) of females in each reproductive status class and 2) the proportion of mature females that were gravid. Catch per unit effort was calculated as the number of yellow perch collected during each trawl divided by the duration of each trawl (in minutes; typically 10) multiplied by 60, so that CPUE was expressed as catch per hour. Because different vessel-gear combinations were used, systemic error could be introduced if CPUE data were combined across vessels. To account for this error, previously determined correction factors for vessels used by both the Ohio Division of Wildlife and USGS Lake Erie Biological Station were applied to the data (Tyson et al. 2006). The second catch metric, the proportion of mature females that were gravid, was calculated by dividing the number of gravid females caught each week by the total number of mature female yellow perch caught each week (i.e., total of gravid, spawning, and spent females). Immature fish were excluded from this analysis.

The change over sample weeks in the presence of gravid females was used to infer the timing of yellow perch spawning in the western basin. Initially, CPUE for immature, gravid, spawning, and spent females for 50 mm total length groups was plotted for each week. These plots were used to visually assess the initiation and relative peak week of spawning in each year and also allowed me to assess if any size-related patterns in spawning existed (i.e., do large females always spawn before smaller females?). Next, I used the GENMOD procedure in the Statistical Analysis System version 9.1.3 (SAS 2005) to conduct logistic regression and determine if the relationship between spawning and water temperature differed across years. The dependent variable of interest in this statistical analysis was the proportion of mature females that were gravid while the independent variable was water temperature.

For the purpose of logistic regression, each mature female was further classified using a binary response variable (1=gravid; 0=spawning or spent). The logistic model was chosen to analyze these data because it provides estimates that must lie in the range between zero (spent) and one (gravid), it does not require any of the assumptions of ordinary least-squared statistics (i.e., normality, linearity, homoscedasticity, etc.), and it can handle non-linear relationships, as it applies a non-linear log transformation to the predicted odds ratio. This analysis was conducted separately for each year. Across years, I compared the probability of collecting gravid females at specific water temperatures (8, 10, and 12˚C) by comparing 95% confidence intervals, generated from logistic regression, to determine if the relationship between water temperature and the initiation and progression of spawning (defined by the proportion of females that were gravid) differed across years.

Results

Water Temperature

Spring air and water temperatures varied substantially among years during this study, which included the warmest spring on record for Ohio (i.e., 2012). While the water temperature warming rate during April-May was not significantly different across years (P=0.67), overall spring water temperatures differed across years (P<0.001) with 2012 and 2010 being warmer than 2011 (2010 vs. 2011: P=0.01; 2011 vs. 2012: P<0.001; 2010 vs. 2012: P=0.11; Fig. 1).

Yellow Perch Spawning Phenology

Weekly CPUE for immature, gravid, spawning, and spent females for 50 mm length groups varied across years (Fig. 2 – 4). In 2010, the first evidence of spawning (i.e. collecting females that were flowing or spent) occurred in Week 2 April (Fig. 2). Spawning continued for about 3 weeks, during which most of the largest females in the sample were spent, whereas smaller females comprised a mixture of gravid and spent (Fig. 2). By Week 1 May, most collected females were classified as spent (Fig. 2).

In 2011, as in 2010, the first evidence of spawning occurred in Week 2 April, when a small portion of collected females in size groups 201-250 mm and 251-300 mm were classified as flowing (Fig. 3). In contrast to 2010, there was no evidence of spawning (i.e. no flowing or spent females) during Week 3 April and only a small proportion of females were spent in Week 4 April. The first evidence of large females spawning occurred in Week 1 May. By Week 2 and 3 May, all collected females were spent except for a portion of 151-200 mm females who remained gravid (Week 2) and flowing (Week 3; Fig. 3). Compared to 2010, this represents a slightly longer spawning period.

In 2012, as in 2010 and 2011, we saw evidence of spawning in a small proportion of females collected in Week 2 April (Fig. 4). Spawning continued over the following week, but was complete by Week 2 May, when all females collected were spent (Fig 4). Compared to 2010 and 2011, this was a shorter duration of the spawning period.

The relationship between spawning and spring water temperature, as determined from logistic regression, was similar in 2010 and 2011 (Fig. 5), despite the fact that these water temperatures occurred at slightly different times in the two years. In 2011, warming occurred later than in 2010. In response, yellow perch delayed spawning in 2011 and spawned during the same temperature range as in 2010 (Fig. 1). In 2012, spring warming occurred earlier than in 2010. In response to earlier warming yellow perch did not initiate spawning at the same temperatures as in 2010 and 2011. Instead female yellow perch initiated spawning at warmer temperatures in 2012, compared to 2010 and 2011. Also in 2012, spawning occurred over a much narrower range of water temperatures than in 2010 and 2011. In 2012, females were more likely to be gravid at 8ºC and 10ºC and less likely to be gravid at 12ºC than at the same temperatures in 2010 and 2011 (Fig. 5).

Discussion

Water Temperature and Yellow Perch Phenology

The timing of spawning appears to be relatively consistent across years, with peak spawning occurring between Week 3 April and Week 1 May. Within this time period, results indicate that Lake Erie female yellow perch may delay spawning until early May during cold springs, waiting for temperatures to increase to ~7-8 ˚C. In contrast, results indicate that in the warmest springs, Lake Erie yellow perch may not spawn earlier (i.e., before Week 3 April), but instead initiate spawning at similar times as in normal years, but at warmer temperatures (~9-10 ˚C). Taken together, findings may indicate that Lake Erie yellow perch may have a minimum date before which spawning cannot occur. After this date has passed, spawning appears to be dependent on temperature.

Freshwater and Anadromous Fish Species

Results may offer a contrast to those from other freshwater and anadromous fish species, which have initiated spawning earlier in response to increasing water temperatures. The timing of European grayling spawning has shifted to 3-4 weeks earlier over the past 60 years, which correlated with a similar increase in water temperatures over this time period (Wedeking and Kung 2010). In addition, earlier spawning migrations in response to rising river temperatures have been documented in Alaskan pink salmon (Taylor 2008), Atlantic salmon through the northeastern United States (Juanes et al. 2004), and in Columbia River sockeye salmon (Crozier et al. 2011). Specifically, in the Columbia River, sockeye salmon have been observed to spawn earlier despite the fact that earlier spawning causes negative effects such as lost feeding opportunities in the ocean, increased harvest, predation, or injury in holding pools, and higher energetic costs of spending the summer in warm water without food (Crozier et al. 2011).

Another North American resident freshwater fish, the brook trout, also may delay spawning in regard to increased water temperatures. However, this species spawns in the fall, and increased summer water temperatures were correlated with a delay in spawning, reduced gonadal development, and a decrease in the total number of redds, or nests, in the study system (Warren et al. 2012). Thus, the timing of brook trout spawning appears to be temperature dependent, resembling the other freshwater and anadromous species discussed above.

Marine Fish Species

Studies have shown that marine fish populations may not respond uniformly to temperature change (Genner et al. 2009). A study in the North Sea between 1990 and 1999 found warming water temperatures initiated spawning among 27 different marine fish species (Greve et al. 2005). In contrast, Genner et al. (2009) found no evidence that spring temperatures were significant predictors of the timing of spring spawning species around Plymouth, England in the North Sea. March temperatures, however, were reliable predictors of the timing of appearance of larvae from summer-spawning species. This difference between summer- and spring-spawners may be due to temperature effects on the rate of gonadal maturation. In Atlantic cod, the timing of spawning could be directly related to oocyte diameter that is governed by temperature-dependent rates of vitellogenesis (Kjesbu 1994).

Possible Explanations

Several potential mechanisms may explain the fact that yellow perch do not spawn early in response to earlier arrival of spring warming. Initiation of yellow perch spawning may be somewhat dependent on photoperiod (duration of daylight; Dabrowski et al. 1997), or complex relationships between winter temperature and egg development (as has been documented for both summer- and spring-spawners in the North Sea [Genner et al. 2009] and Atlantic cod [Kjesbu 1994]) may be at work. Regardless of the cause, the inability of yellow perch to spawn earlier could have negative consequences for offspring if the timing of emergence does not match peak spring abundance of prey resources (match/mismatch hypothesis; Hjort 1914; Cushing 1990), i.e. if prey are responding to early warming, but yellow perch are not.

Study Limitations

One limitation of my study was that logistical constraints limited sampling opportunities in 2012 as compared to 2010 and 2011, when trawling was conducted more frequently. Bottom trawling was only conducted four times in 2012, with two sampling dates composed mostly of gravid females and the other sampling dates composed mostly of spent females (Fig. 4). An additional sampling event conducted between these two groups would have provided more data on the progression of yellow perch spawning as it related to temperature and may have resulted in a more accurate and precise logistic relationship for 2012.

Additionally, most of the other fish species referenced for comparison herein are either riverine freshwater species or marine species. Research on similar lentic freshwater fish species might provide additional insight into the generality of my results for yellow perch spawning.

Conclusions and Recommendations

Yellow perch appear not to initiate spawning earlier in response to warming water temperatures, but instead may have a minimum date before which spawning cannot occur. If prey species emerge earlier in response to warming temperatures, yellow perch offspring survival, and, subsequently, recruitment may be low if the timing of emergence does not match.

Further research investigating the effects of environmental variables on the phenology of reproductive events may provide insight into mechanisms underlying the lack of response of yellow perch spawning to early spring warning. Specifically, future studies that synthesize data from previous yellow perch experiments and field collections to further understand how temperature and photoperiod influence timing of spawning may be insightful. In addition, a study of autumnal phenological events (i.e., temperature effects on the start of vitellogenesis) might provide insight into mechanisms underlying my results. For example, determining if yellow perch require a set duration of time for eggs to fully develop before spawning can occur, as it does for Atlantic cod (Kjesbu, 1994). Certainly, continued efforts to understand the effects of environmental variables on phenotypic events will provide insight into how this economically and ecologically important specie will react to climate change.

Literature Cited

Barson, N. J., T. O. Haugen, L. A. Vøllestad, and C. R. Primmer. 2009. Contemporary isolation by-distance, but not isolation-by-time, among demes of European grayling (*Thymallus thymallus,* Linnaeus) with recent common ancestors. Evolution 63:549–556.

Beaugrand G., K. Brander, J. A. Lindley, S. Souissi, and P.C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature Journal 426:661–664.

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: A case study of a shift toward earlier migration date in sockeye salmon. The American Naturalist 178:755-73.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293.

Dabrowski K., R.E. Ciereszko, and A. Ciereszko. 1997. Effects of temperature and photoperiod on reproduction of female yellow perch *Perca flavescen*s: plasma concentrations of steroid hormones, spontaneous and induced ovulation, and quality of eggs. Journal of the World Aquaculture Society 28:344-356.

Durant, J. M., D. O. Hjermann, G. Otterson, and N. C. Stenseth. Climate and the match or mismatch between predator requirements and resource availability. 2007. Journal of Climate Research 33:271-283.

Genner, M. J., et al. 2009. Temperature-driven phenological changes within a marine larval fish assemblage. J. Plankton Research 32:699-708.

Greve, W., Prinage, S., Zidowitz, H. et al. 2005. On the phenology of North Sea ichthyoplankton. ICES J. Mar. Sci. 62:1216–1223.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp p-v Réun Cons Int Exp Mer 20:1–228.

Juanes, F., S. Gephard, and K. F. Beland. 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. Canadian Journal of Fisheries and Aquatic Sciences 61:2392–2400.

Kayes, T. B., and H. E. Calbert. 1979. Effects of photoperiod and temperature on the spawning of yellow perch (*Perca flavescens*). Proceedings of the World Mariculture Society 10: 306-316.

Kjesbu, O. S. 1994 Time of start of spawning in Atlantic cod (Gadus morhua) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. J. Fish Biol. 45:719–735.

Magnuson, J. J. 2010. History and heroes: the thermal niche of fishes and long-term lake ice dynamics. Journal of Fish Biology 77: 1731-1744.

Taylor, S. G. 2008. Climate warming causes phenological shift in pink salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. Global Change Biology 14:229–235.

Treasurer, J.W. and F.G.T. Holiday. 1981. Some aspects of the reproductive biology of perch *Perca fluviatilis L.* A histological description of the reproductive cycle. Journal of Fish Biology 18:359-76.

Turner, T. F., T. J. Krabbenhoft, and A. S. Burdett. 2010. Reproductive phenology and fish community structure in an arid-land river season. American Fisheries Society Symposium 73:427-446.

Tyson, J. T., T. B. Johnson, C. T. Knight, and M. T. Bur. 2006. Intercalibration of research survey vessels on Lake Erie. North American Journal of Fisheries Management 26:559 570.

Walther G. R., et al. 2002. Ecological responses to recent climate change. Nature Journal 416: 389-395.

Warren D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon, and C. E. Kraft. 2012. Elevated summer temperatures delay spawning and reduce red construction for resident brook trout (*Salvelinus fontinalis*). Global Change Biology 18:1804-1811.

Wang, J., X. Ai, H. Hu, A. Clites, M. Colton, and B. Lofgren. 2012: Temporal and Spatial Variability of Great Lakes Ice Cover, 1973–2010. J. Climate, 25, 1318–1329.

Wedeking, C., and C. Kung. 2010. Shift of spawning season and effects of climate warming on developmental stages of a grayling (Salmonidae). J. Cons. Bio. 24:1418-423.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49: 2196-2218.

Fig. 1. Average (± S.E.) water temperatures (°C) measured during weekly sampling trips conducted in April and May, 2010-2012

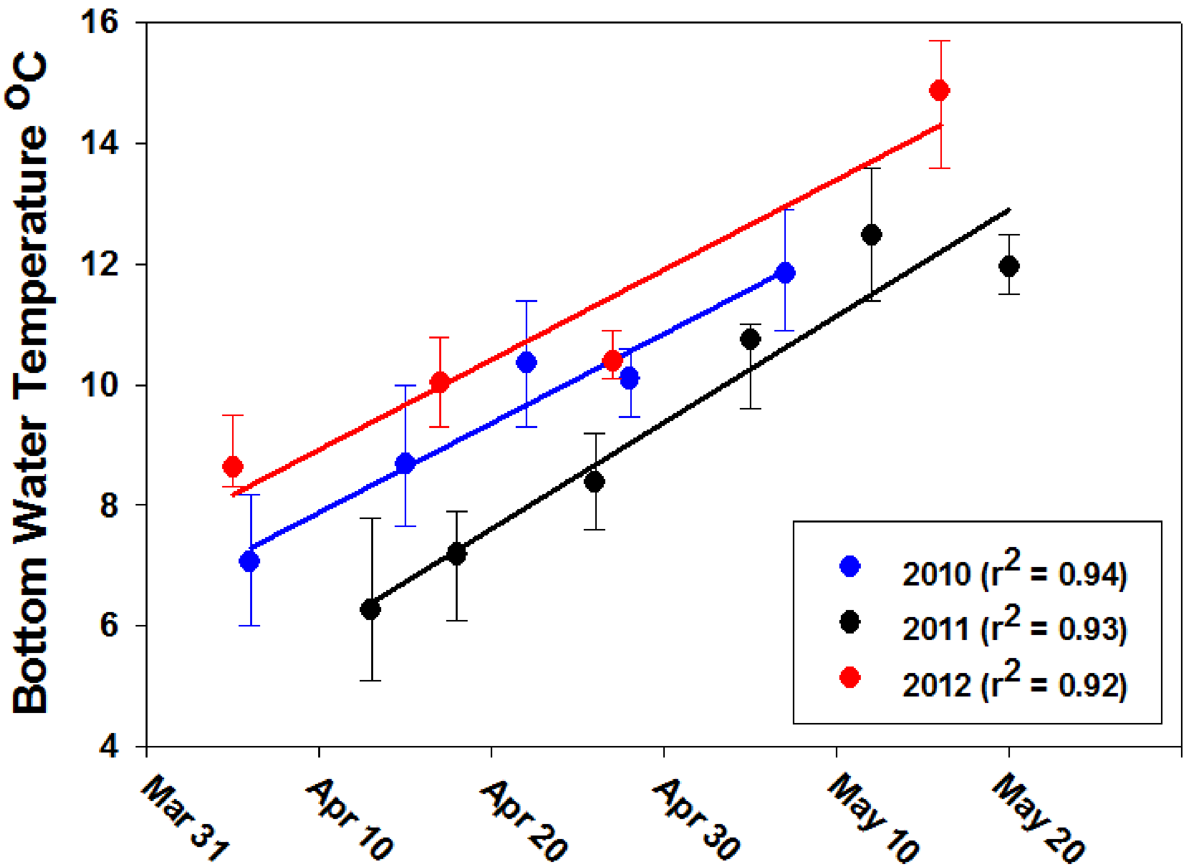

Fig. 2. Catch per unit effort (CPUE; unit effort = 1 hour bottom trawling) for female yellow perch classified as immature, gravid, flowing, or spent during weekly sampling trips in 2010. Data is presented in 50 mm size-groups.

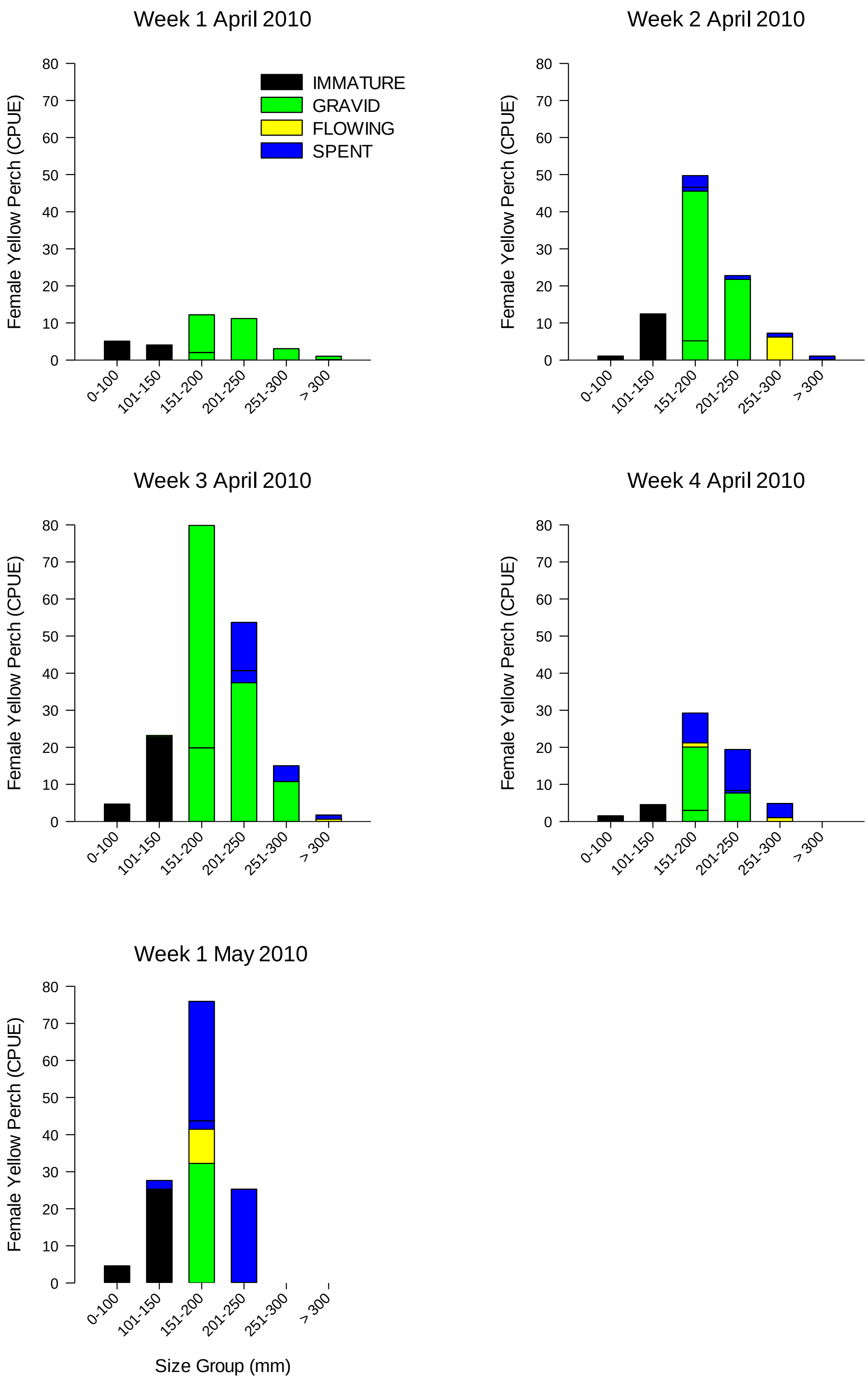

Fig. 3. Catch per unit effort (CPUE; unit effort = 1 hour bottom trawling) for female yellow perch classified as immature, gravid, flowing, or spent during weekly sampling trips in 2011. Data is presented in 50 mm size-groups.

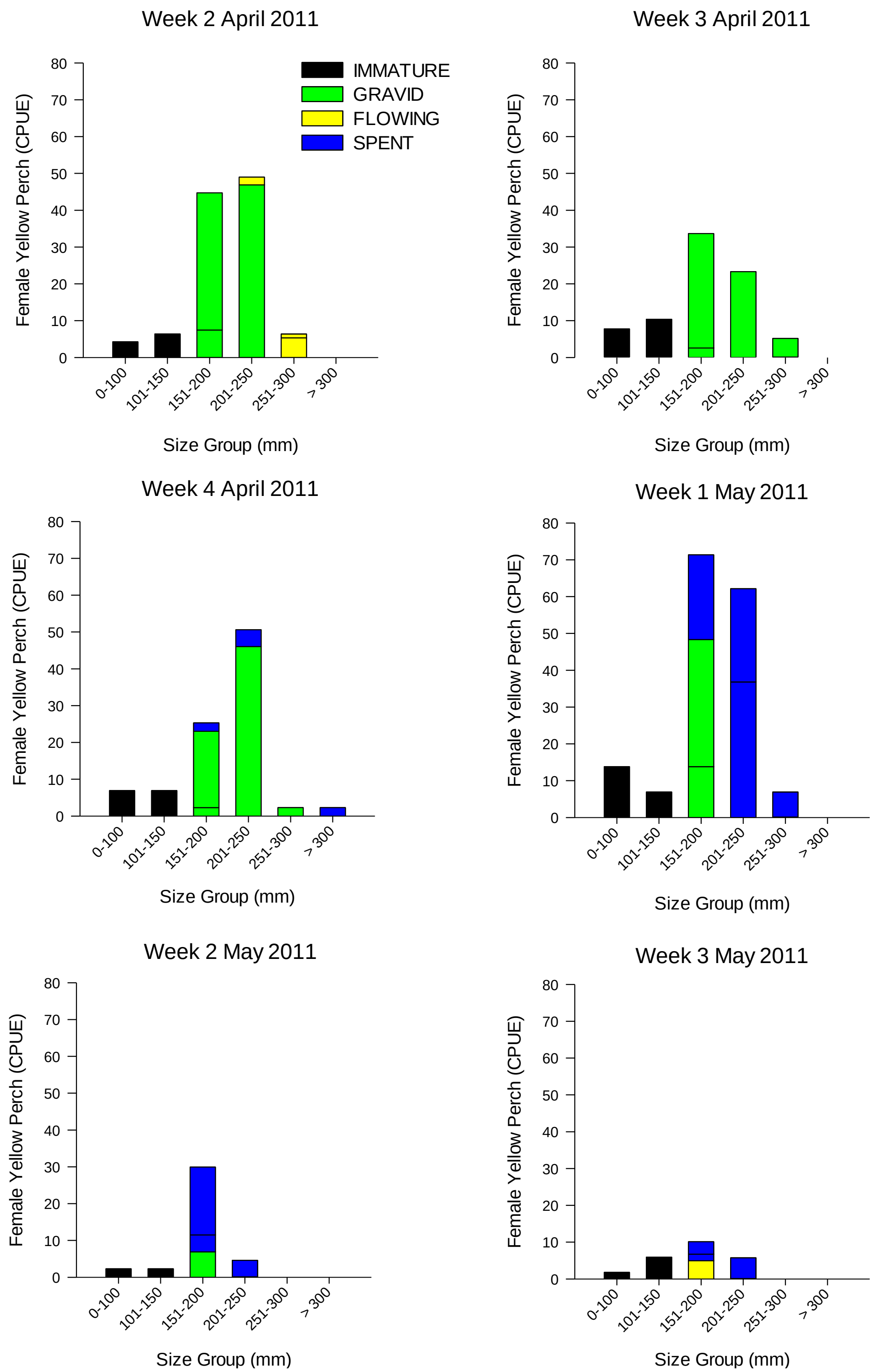

Fig. 4. Catch per unit effort (CPUE; unit effort = 1 hour bottom trawling) for female yellow perch classified as immature, gravid, flowing, or spent during weekly sampling trips in 2012. Data is presented in 50 mm size-groups.

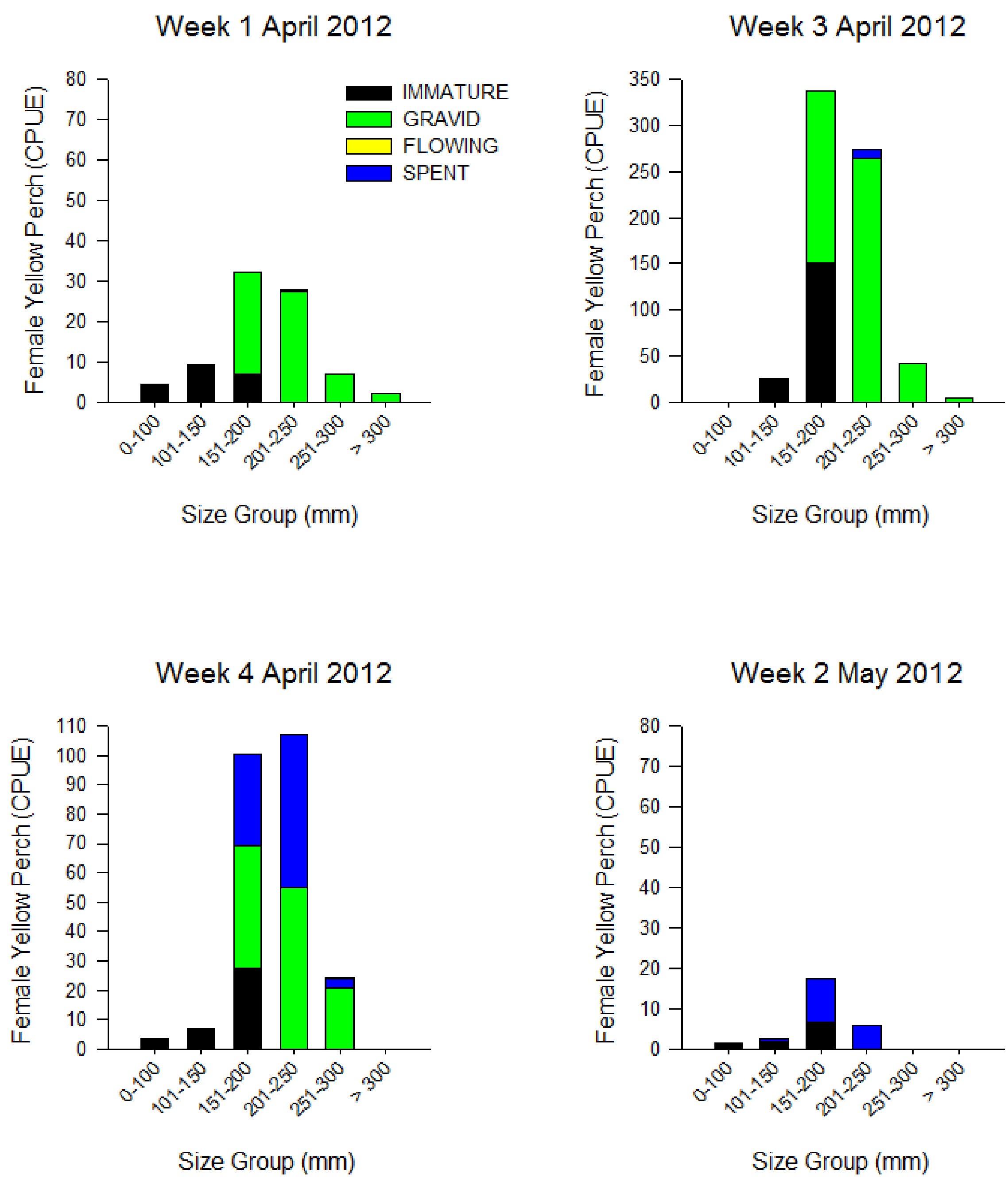

Fig. 5. Probability that a mature female collected from the western basin of Lake Erie in the spring has not yet spawned as a function of water temperature in 2010, 2011, and 2012. Dashed line = 95% confidence interval. Points on the graph with the same letters (a-f) have probabilities that are not significantly different.